ECOLOGICAL CHARACTERISTICS OF CORAL PATCH REEFS AT MIDWAY ATOLL, NORTHWESTERN HAWAIIAN ISLANDS

BY

ROBERT E. SCHROEDER[1] AND JAMES D. PARRISH[2]

ABSTRACT

Ecological aspects of coral patch reefs were studied from 1981 to 1985 in Welles Harbor, Midway Atoll. Water temperatures varied from 17°C in February to 28°C in August. Sizes of reefs studied were described by mean area (59 m^2), mean volume (52 m^3), vertical relief (<1 m), and inter-reef isolation (100 m). Considerable temporal change in reef size occurred due to large winter swells shifting bottom sand. Six common species accounted for 70% of all individual fish visually censused over 4 years. Overall fish assemblage composition ranged from 11 to 46 fish/10 m^2, from 3 to 14 species. Numerical abundance and species richness for all fish (pooled) strongly correlated with physical reef substrate characteristics of area, volume, and vertical relief during summer. Species diversity (H') was not correlated with the substrate variables, suggesting similarity in the structure of fish communities among different sizes of patch reefs. Daily surveillance for presence of large transient taxa suggested that visits by sharks, large jacks, monk seals, sea turtles, and dolphins were infrequent. Density estimates were made for all conspicuous invertebrate megafauna during initial and final assessments. Six common taxa provided 90% of these counts; nearly half were sea urchins. Percent cover also was recorded for coral and algal species on the patch reefs. Cover by live coral was low (about 7%) and dominated by a few species. Mean algal cover ranged from 32 to 77%. Such information on ecological characteristics of reefs may aid in understanding complex ecological processes and provides an earlier reference for current ecosystem studies.

INTRODUCTION

Coral reef communities are among the most ecologically diverse systems known, including many ecological interactions among fish, coral, other invertebrates, and algae (Hixon, 1997). Many coral reefs are patchy in spatial distribution. Abiotic and biotic factors of the reef environment can affect the distribution patterns of fish assemblages (Hobson, 1980; Sale, 1980; Friedlander and Parrish, 1998). These factors include reef structural attributes (e.g., reef size, substrate complexity, patch isolation, and depth),

[1]Joint Institute for Marine and Atmospheric Research and NOAA Pacific Islands Fisheries Science Center, 1125B Ala Moana Boulevard, Honolulu, HI 96814 USA, E-mail: Robert.Schroeder@noaa.gov
[2]U.S. Geological Survey, Hawaii Cooperative Fishery Research Unit, 2538 The Mall, University of Hawaii at Manoa, Honolulu, HI 96822 USA

environmental variables (e.g., water temperature, suspended sediment, current, and sand movement), and direct or indirect effects of other biota (e.g., algae, corals, other invertebrates, and nonteleost vertebrates) (Luckhurst and Luckhurst, 1978; Bohnsack, 1979; Carpenter et al., 1981; Sale and Douglas, 1984; Walsh, 1985; Green et al., 1987; Roberts and Ormond, 1987; Clarke, 1988; DeFelice and Parrish, 2001, 2003). Behavioral interactions among fishes, such as predation and competition, also can influence the abundance of these populations, as well as benthic community structure (Sale, 1980; DeMartini and Friedlander, 2006).

Reef fish communities from the geographically isolated Hawaiian Archipelago are characterized by low species richness, high endemism (~21% of the inshore species, many of which are abundant, and increasing with latitude), and the presence of mesoscale eddies, which may help retain planktonic larvae (Gosline and Brock, 1960; Lobel and Robinson, 1986; Hourigan and Reese, 1987; Lobel, 1989; Randall, 1996; DeMartini and Friedlander, 2004; Firing et al., in press). Most species are small and site-attached or have limited home ranges. All trophic guilds are represented, although most species are generalists, exhibiting wide diet overlap (Hobson, 1974; Sale, 1980; Parrish, et al., 1985).

Patch reefs are natural habitat structures composed of coral and rock substrate that are isolated across sand from other reefs. They are usually of small to moderate size (e.g., < 100 m across), but numerous in many shallow nearshore environments. Patch reefs are valuable for some ecological studies because they support relatively isolated communities with diverse and abundant fauna, and are of manageable size for assessment with replication (Nolan, 1975; Sale, 1980, 1984; Clarke, 1988; Ault and Johnson, 1998). Some investigators have assumed they are closed systems (following larval settlement) and that they reveal patterns representative of much larger reefs (Smith and Tyler, 1975; Jones and Chase, 1975). However, the validity of these assumptions has been questioned (Clarke, 1988; Robertson, 1988; Ault and Johnson, 1998; Schroeder and Parrish, 2005). The degree of isolation between patch reefs can affect migration rates by fish that are not fully site attached. Some species use small patch reefs only as a juvenile nursery habitat before relocating to more extensive reefs.

The present study describes the structure of fish communities and related ecological characteristics of 'natural' patch reefs within the lagoon at Midway from 1981 to 1985. Midway is a high-latitude coral atoll characterized by: 1) isolation in the mid-Pacific, 2) a subtropical climate, with a wide seasonal water temperature range, 3) many species that are common on shallow reefs and attain large sizes in the NWHI, but occur only rarely or in deep water farther southeast, and 4) lagoon reefs that are essentially free of fishing pressure (Gosline & Brock, 1960; Mauck, 1975; Hobson, 1980, 1984; Randall et al., 1993; Friedlander and DeMartini, 2002). These reefs and their associated communities were generally representative of a protected inshore biotype, common in the northwestern portion of the Hawaiian Archipelago.

METHODS AND MATERIALS

Study Area

Coral patch reefs were studied during 1981-1985 within Welles Harbor, in the SW quarter of Midway Atoll (centered about 28°12' N latitude, 177°24' W longitude) of the Northwestern Hawaiian Islands (NWHI) (Fig. 1). Midway, located at the northern limit of the subtropics, experiences more pronounced seasonal extremes than the lower latitude (19° N to 22° N latitude) high Hawaiian Islands, some 2,000 km to the SE. The lagoon averages 10 km in diameter and is surrounded by a barrier reef except along the W and NW sides. The four patch reefs studied were among many scattered within the SW section (~2 km W of Sand Island and ~2 km E of the western barrier reef) of the shallow (5-10 m), sand-bottom lagoon. These 'natural' patch reefs were selected based on general similarity in broad characteristics (e.g., size, substrate composition, vertical relief, water depth, isolation across sand, and apparent fish assemblage composition) with those occurring within the Welles Harbor study area. While parts of the Midway Islands and its lagoon had experienced major disturbances in previous decades (e.g., harbor dredging, landfill, and marine recreation by U.S. Navy personnel), the reefs in the section of the lagoon for this study had experienced no known recent fishing disturbance (pers. comm., Midway Koral Kings Dive Shop). Measured water temperatures at Midway ranged from 17°C in February to 28°C in August. Currents were usually negligible or slight from the south (i.e., rarely ≥ 1 knot) .Large oceanic swells from the NW often created strong bottom surge during winter. Underwater horizontal visibility was usually 10-20 m, except when rare storms greatly increased turbidity.

Figure 1. Typical coral patch reef (station 3C) in Welles Harbor, Midway Atoll (Photo: R. Schroeder).

Reef Physical Characteristics

Major physical attributes of each patch reef were measured at the beginning of the study (July-August 1981 and July-August 1982), and repeated during the final sampling period (July-August 1985). Initial attributes of two replacement reefs (for originals covered by sand during the winter of 1983-84) were measured in August 1984 (see Results and Discussion). Reef physical characteristics were measured because major differences in patch reef size and structure could significantly influence the composition of the fish community (Helfman, 1978; Sale and Douglas, 1984; Clarke, 1988). Also, significant temporal changes in the reef substrate could affect other ecological characteristics.

Reef Size. Detailed bathymetric maps were sketched by divers measuring depth with accurate gauges, providing a vertical reef profile referenced to a standardized (1x2 m), horizontal rope grid set over the entire reef. From these maps, the projected surface area (two-dimensional footprint of hard substrate) of each reef was estimated by summing the areas of all grid cells. Volume was estimated by multiplying the projected area increment between each two adjacent depth contours by the height of the increment above the sand at the base of the reef, and summing the products.

Reef Complexity. An index of reef substrate complexity, “vertical relief,” was estimated for each reef following Luckhurst and Luckhurst (1978). Over each patch reef, sets of parallel horizontal lines, 1-m apart, were constructed that touched the highest point of the reef along each line. Vertical measurements were taken from these lines to the reef surface at 0.5-m intervals along each line. Vertical relief was reported as the mean of these measured distances. We also conducted Luckhurst’s “substrate rugosity” chain-measured surface-contour/linear distance method to assess substrate complexity, but this measure was not used in our analysis since the interpretation was confounded for patch reefs of varying size.

Reef Isolation. An index of patch reef isolation was obtained by measuring distances to the nearest neighboring reefs in eight directions (one within each octant around the patch reef), taking the mean of these eight measurements, and then taking the mean of that value and the single measurement to the nearest neighboring reef. This strong weighting of the arbitrary index in favor of the closest reef seemed appropriate ecologically (e.g., may enhance fish migration via a visual stepping-stone effect) (Schroeder, 1987; 1989b).

Reef Ecological Characteristics

Reef Fish Community Assessment. The total-count underwater visual census method was used to quantify species composition, abundance, and temporal variability of resident fish populations on each patch reef (Schroeder and Parrish, 2005). The total number of all diurnally observable individuals of each species was recorded, separated into visually estimated size classes of fish standard length (SL), for subsequent analysis.

The patch reefs were of manageable size to permit total fish counts, as opposed to transect subsampling. Size classes were: 1-2 cm, 3-4 cm, 5-6 cm, 7-10 cm, 11-15 cm, and then each consecutively higher 5 cm class. Estimates of individual fish size were aided by reference to a calibrated 20-cm rule along the top of the underwater data form. Validation was tested periodically by comparing estimated length to actual length of individual fish speared by each observer far from the study area; estimates were highly accurate (e.g., nearly all $r^2 > 0.80$, $P < 0.001$; Schroeder, 1989a). Censuses were conducted between 0800 and 1700 h during the 20 major (2-6 wk) 'survey periods' (i.e., continuous daily sampling periods) of May 1981-August 1985 (i.e., May-Jun81, Jul-Aug81, Jan82, May-Jun82, Jul-Aug82, Nov82, Dec/Jan83, Mar83, May-Jun83, Jul-Aug83, Nov83, Dec/Jan84, Mar84, Jun-Jul84, Aug84, Oct-Nov84, Jan85, Mar-Apr85, May85, Jul-Aug85). During each survey period, the census was replicated 2 to 10 times on each reef, with rare exceptions.

Assessment of Other Reef Biota. Common species of other resident reef biota (e.g., algae, corals, noncryptic invertebrates) at each station were visually assessed, using the standard 1x2-m grid, during the same periods (initial and final) that reef physical characteristics were measured. Data recorded included the estimated percent cover of substrate surface by each major algal and coral taxon within a grid cell, and the number of discrete, nonsessile macroinvertebrates counted per cell. The mean of values from all grid cells in a reef was used to represent the reef.

Other Ecological Characteristics. Mean daily frequencies for sightings of large, highly transient fishes and other marine vertebrates were recorded from May 1980 to August 1985. Taxa considered were carcharhinids (sharks), carangids (jacks), Rajiformes (rays), *Monachus schauinslandi* (Hawaiian monk seal), *Chelonia mydas* (green sea turtle), and *Stenella longirostris* (spinner dolphin). Shark and jack frequencies were calculated based on all diurnal periods per survey period during which research activities were conducted on the focal set of natural study reefs. (Observation time in the water was roughly the same for most days.) Daily records of the other large vertebrate taxa were made during any time of the day in or on the water of the Welles Harbor study area; observation time for these sightings was less standardized. Notes on behavioral patterns also were recorded for common fishes.

Fish-Physical Correlations

Spearman rank correlation analysis was used to search for associations of the major physical patch reef characteristics with the fish community. Reef characteristics used were substrate area, volume, and vertical relief (measured as described above). Characteristics of the fish community used were species richness, measured by the mean number of species censused on a reef during a survey period, the Shannon-Weaver species diversity index (H'), which incorporates both species richness and abundance (Shannon and Weaver, 1949), the numerical abundance of all (pooled) species, and the numerical abundance of several common (abundant) species, all from visual census data. (For the group of common species, the significance of the correlations was based on the experimentwise error rate [Miller, 1981].)

RESULTS AND DISCUSSION

Reef Physical Characteristics

Reef Size. Patch reef area ranged from 12-186 m^2 (mean 58.8 m^2) and volume from 4-155 m^3 (mean 52.2 m^3) (Table 1). During the 4-year study, the size of some reefs changed when shifting sand either exposed or buried hard reef substrate. For example, around some reefs, water depth to the lagoon floor was reduced from 10 m to 5 m in <2-mo. time. Long, steep slopes of sand marked the transition between shallow and deep areas, somewhat analogous to wind-driven terrestrial sand dunes. During the winter of 1983-84, two study reefs ($3C_1$ and $4C_1$) were buried completely, and study sites had to be replaced with other patch reefs nearby (3C and 4C). These changes in reef size resulted from the combined effects of severe winter storms, tides, and related currents. High energy, large wave events from the NW originate during extratropical north Pacific winter storms and subject NWHI shallow-water coral reef communities to wave energy an order of magnitude greater than typical winter waves (Friedlander, et al. 2005). The

Table 1. Summary of patch reef size (area and volume), and vertical relief (mean±sd) as an estimate of substrate complexity (N= 61-183 total measurements per reef), at the beginning and end of the study.

	Period						Change		
	Initial			Final					
	Area (m^2)	Volume (m^3)	Relief (cm)	Area (m^2)	Volume (m^3)	Relief (cm)	Area (%)	Volume (%)	Relief (%)
Station:									
1C	12.2	4.4	34.1(19.2)	10.9	6.2	38.4(15.8)	-10.1	39.1[2]	12.6
2C	50.0	56.7	60.9(44.0)	22.6	10.0	37.1(19.9)	-54.9	-82.4	-39.1
3C[1]	39.0	24.0	67.7(46.3)	52.2	66.9	92.3(54.9)	34.0	178.8	36.8
4C[1]	185.6	154.9	72.8(41.9)	151.0	146.1	62.4(43.1)	-18.6	-5.7	-14.3

[1)] Initial start times for stations 3C and 4C were later in the study, after the originally selected reefs ($3C_1$ and $4C_1$) were totally buried by progressive sand movement during winter storms.
[2)] The inconsistent directions of change for area and volume may be a consequence of the small sample size compounded by the low precision of estimating volume from area maps, and by different observers.

magnitude of sand movement across lagoon floors and other shallow habitats, its effects on patch reef size and complexity, and its significance for ecological communities have been reported rarely (Yamanouchi, 1988; Mizamura et al., 2000). These changes in the sizes of patch reefs prevented straightforward analysis and comparison of different reefs on the basis of fish density.

Reef Complexity. The study patch reefs had roughly similar substrate, predominantly dead eroded coral (mainly *Porites lobata* and *P. compressa*), which retained much of the original colony morphology. Substrate complexity, measured as mean (±sd) vertical relief per reef, ranged from 0.34 (±0.19) m to 0.92 (±0.55) m (3 m maximum) (Table 1). These means varied spatially and temporally during the study, due to shifting sand; some stations became more complex while others became less so.

Reef Isolation. Sand flats surrounding our study reefs at depths of 6-10 m had little unconsolidated rubble. Inter-reef isolation (to nearest neighbor patch reef) was 123 m for reef 1C, 132 m for reef 2C, 71 m for reef $3C_1$, and 74 m for reef $4C_1$ (mean 100 [±32] m). These reefs were believed initially to be sufficiently isolated from neighboring patches that individual reefs functioned more or less as incongruous ecological communities. However, results of our subsequent experimental work at this site indicated that small, semi-resident piscivores (e.g., lizardfish) move more widely among patch reefs than had been recognized (Schroeder and Parrish, 2005).

Reef Ecological Characteristics

Fish Communities. Considering overall diurnal, non-cryptic fish assemblage composition of all patch reefs studied, the average minimum number (i.e., exclusive of short-lived major settlement pulses) and species richness ranged from about 15 species (50 fish) on the smallest patch reef (12 m^2), to about 50 species (200 fish) on the largest reef (186 m^2). Our values for fish species richness were similar to those found by Molles (1978) on comparable size patch reefs in the Gulf of California. They were higher than those found by Walsh (1983) on the fringing reef along the Kona coast of Hawaii (15 species [mean of 70 fish] on 25m^2 quadrats), and lower than those found by Jones and Chase (1975) on large, lagoonal patch reefs of Guam (67 species [1859 fish]; total transect area of 1400 m^2).

For each species/taxon, its percent numerical abundance (relative to the total), percent occurrence (in all censuses), and estimated size range are listed in Table 2. Consistent with studies from other geographic regions, we found that only a few species provide the bulk of the reef fish community. *Pervagor spilosoma* (Monacanthidae, filefish), *Apogon maculiferus* (Apogonidae, cardinalfish), and *Dascyllus albisella* (Pomacentridae, damselfish), which each composed ~15% of the total abundance (Table 2), were characterized by major seasonally and annually variable settlement pulses. They dominated the juvenile census counts and had the highest settlement rates of all fishes (Schroeder, 1985, 1989a). *Thalassoma duperrey* (Labridae), *Stegastes fasciolatus* (Pomacentridae), and *Chromis ovalis* (Pomacentridae) each provided an additional ~8% of the total number of fish, and also settled in considerable numbers on the patch reefs. These six common species accounted for 70% of all fish individuals visually censused on these reefs (135 total fish species/taxa). The low faunal diversity, which is characteristic of Hawaiian reefs (Randall et al., 1993), combined with strong settlement strategies by a few species (e.g., Sale, 1985; Walsh, 1985; Schroeder, 1985, 1989a), probably accentuates the numerical dominance of the fish community by several species at Midway. Similarly, Sale and Douglas (1984) found that apogonids, pomacentrids, and gobioids dominated small patch reefs of the Great Barrier Reef. Walsh (1983) found that

Table 2. Composition of the fish community as indicated by visual census, showing percent relative numerical abundance (Total N = 90,103 individuals, 135 species/taxa) and percent frequency of occurrence (in N = 20 total survey periods) for 95% of all (cumulative) fish censused, based on pooled data from four natural patch reefs from May 1981 to August 1985. (The off-reef, sand-rubble dwelling goby *Gnatholepis anjerensis* that was ubiquitous in late summer is considered separately.)

Species/taxa:	Abundance %	Occurrence %	Size Range (cm SL) (Min.-Max.)
Pervagor spilosoma	15.47	60	3-15
Apogon maculiferus	14.64	100	1-15
Dascyllus albisella	14.52	100	1-10
Thalassoma duperrey	8.14	100	1-25
Stegastes fasciolatus	8.05	100	1-10
Chromis ovalis	7.64	100	1-15
Scarid spp.	3.04	95	1-15
Apogonid spp.	2.78	40	1-20
Chaetodon miliaris	2.23	100	1-20
Labroides phthirophagus	1.96	100	1-10
Spratelloides delicatulus	1.78	5	3-4
Stethojulis balteata	1.50	100	1-30
Sebastapistes coniorta	1.42	95	1-20
Thalassoma ballieui	0.96	100	1-40
Canthigaster jactator	0.92	100	1-15
Syndontid spp.	0.83	100	1-35
Gymnothorax eurostus	0.81	100	7-100
Chromis hanui	0.81	100	1-10
Scorpaenodes littoralis	0.75	95	1-15
Mulloidichthys flavolineatus	0.71	35	7-25
Cirrhitops fasciatus	0.64	100	1-15
Plectroglyphidodon johnstonianus	0.60	95	1-15
Paracirrhites forsteri	0.59	100	1-20
Dendrochirus barberi	0.59	90	1-25
Mulloidichthys vanicolensis	0.56	35	5-15
Foa brachygramma	0.56	80	1-15
Chaetodon fremblii	0.54	100	1-15
Gymnothorax steindachneri	0.45	100	7-100
Bodianus bilunulatus	0.39	100	1-45

Table 2. Continued.

Species/taxa:	Abundance %	Occurrence %	Size Range (cm SL) (Min.-Max.)
Macropharyngodon geoffroy	0.37	90	1-20
Priacanthid spp.	0.36	50	5-25
Neoniphon sammara	0.33	100	1-25
All others (pooled)* (103 species/taxa, below)	5.00	na	na
Gnatholepis anjerensis (Total separate no. of individuals = 34,541)	100.00	20	1-6

*Additional fish species/taxa accounting for a total of 5% of all censused: *Anampses cuvier, Coris flavovittata, Ctenochaetus strigosus, Myripristis* sp., *Cheilinus bimaculatus, Pseudocheilinus octotaenia, Sebastapistes ballieui, Parupeneus multifasciatus, Brotula multibarbata, Coris venusta, Scarus dubius, Abudefduf abdominalis, Scorpaenopsis diabolus, Sargocentron diadema, Cirrhitus pinnulatus, Pterois sphex, Scorpaenid* spp., *Priacanthus cruentatus, Parupeneus pleurostigma, Arothron hispidus, Synodus ulae, Myripristis kuntee, Anampses chrysocephalus, Doryrhamphus melanopleura, Gobiid spp., Chlorurus perspicillatus, Calotomus* sp., *Enchelycore pardalis, Taenianotus triacanthus, Parupeneus porphyreus, Aulostomus chinensis, Chaetodon auriga, Zebrasoma flavescens, Zanclus cornutus, Naso unicornis, Kyphosus* sp., *Lactoria fornasini, Caracanthus maculatus, Acanthurus triostegus, Gymnothorax undulatus, Labrid spp., Myrichthys maculosus, Teleostei spp., Cheilinus unifasciatus, Paracirrhites arcatus, Chaetodon multicinctus, Cirripectes vanderbilti, Cymolutes lecluse, Cirripectes* sp., *Muraenid* spp., *Cymolutes* sp., *Priacanthus meeki, Antennariid* spp., *Saurida gracilis, Chlorurus sordidus, Priolepis eugenius, Carangoides orthogrammus, Conger cinereus, Anampses* sp., *Fistularia commersonii, Scorpaenopsis cacopsis, Bothus mancus, Calotomus zonarcha, Epinephelus quernus, Ostracion meleagris, Sargocentron* sp., *Naso lituratus, Fusigobius neophytus, Apogon kallopterus, Amblycirrhitus bimacula, Diodon holacanthus, Bothid* spp., *Gomphosus varius, Gymnothorax hepaticus, Ophichthus polyophthalmus, Sargocentron xantherythrum, Acanthurus leucopareius, Acanthurus achilles, Caranx ignobolis, Parupeneus bifasciatus, Chaetodon ornatissimus, Forcipiger flavissimus, Diodon hystrix, Carcharhinus amblyrhynchos, Pomacentrid* spp., *Antennarius coccineus, Priolepis* sp., *Gymnothorax pictus, Caranx sexfasciatus, Caranx melampygus, Centropyge potteri, Pseudocaranx dentex, Seriola dumerili, Gymnothorax flavimarginatus, Blenniid* spp., *Gymnothorax meleagris, Gymnothorax pindae, Novaculichthys taeniourus, Pseudocheilinus* sp., *Chromis verater, Plectroglyphydodon imparipennis, Asterropteryx semipunctatus, Arothron meleagris*

two species of acanthurids and a pomacentrid predominated (>50% of total number of fish) in census counts along the Kona coast of Hawaii. Of the seven most abundant species he recorded there, only two (the wrasse *T. duperrey* and the damselfish *S. fasciolatus*) were among the six most abundant species we censused at Midway, at the opposite end of the Hawaiian Archipelago (Walsh, 1983). Similarity in species abundance rankings between the two locations was low.

Other Reef Biota

Invertebrates. On Midway patch reefs, visible macroinvertebrates were common. Density estimates (as grand mean number of individuals over all censuses counted/m^2) for all (pooled) visible, macroinvertebrate taxa varied from 18.4 $\pm$13.7 (sd) initially, to 30.4 $\pm$24.3 (sd) at the final assessment (Table 3). Six taxa (in decreasing order of abundance) provided over 90% of these numbers: *Echinometra mathaei* (urchin), *Rhynchocinetes* sp. (shrimp), *Diadema paucispinum* (urchin), *Ophiocoma pica* (brittle star), *Echinostrephus aciculatus* (urchin), and *Plakobranchus ocellatus* (sea slug). Half of all these invertebrates counted were *E. mathaei* and *D. paucispinum*. Fish predators on sea urchins include triggerfish, pufferfish, snapper, large wrasse, and porcupinefish (Ormond et al., 1973; Glynn et al., 1979; Carpenter, 1984). Sea urchin densities can greatly increase on heavily fished reefs following reductions of these predators and reduced competition from herbivores (e.g., parrotfish, surgeonfish) (Hay, 1984). Herbivorous damselfish also can exclude sea urchins from their territories (Williams, 1981).

Corals. More than 90% of the substrate of Midway patch reefs was dead, partially eroded coral rock (mostly from *Porites* spp.). The mean percent of total live coral cover (all species pooled) was low: 7.2% ($\pm$8.1 sd), initially, and 6.9% ($\pm$6.6), at the final assessment (Table 4). Only a few species predominated, mainly *Pocillopora meandrina* (3.2%), *P. damicornis* (1.6%), *Porites lobata* (1.4%), *Cyphastrea ocellina* (0.9%) and *Leptastrea purpurea* (0.1%). Nearly 70% of live coral was branching colonies of *Pocillopora* spp., a preferred substrate for settling postlarval damselfish *Dascyllus albisella* (Booth, 1995). On the Great Barrier Reef, the number of a related damselfish congener (*D. aruanus*) inhabiting coral heads exhibited a strong positive correlation with size (area) of the coral colony (Sale, 1972).

Algae. Algal cover on the Midway patch reefs was highly variable seasonally, annually, and spatially. The mean percent of total algal cover (all taxa pooled) on the patch reefs was 76.7% ($\pm$55.5 sd), during the initial summer assessment, and 32.1% ($\pm$35.7 sd), during the final summer sampling period (Table 5). During late summer in some years, a thick, dark algal carpet covered many of the reefs, but very little algae were obvious in winter. Common taxa which collectively composed over 90% of the usual cover were (in order of decreasing abundance) Phaeophyta spp., *Centoceras clavulatum*, *Ralfsia pangoensis*, *Spyridia filamentosa*, *Dictyota* sp., *Lobophora variegata*, *Hydrolithon reinboldii*, Rhodophyta (spp.), and *Lyngbya majuscula*. Schooling herbivores (e.g., parrotfish, surgeonfish) graze reef algae heavily, and can strongly affect the community structure and standing crop of macroalgae on patch reefs (Hixon, 1997). Such activity is important for maintenance of healthy coral reefs because it opens space for settling and growth of new corals. The herbivorous damselfish, *Stegastes fasciolatus*, is common on Midway reefs, where it defends small algal territories and can affect the abundance and local species composition of reef algae (Hixon, 1997). The heavier algal mat resulting from this "gardening" inside territories increases habitat for small reef invertebrates and epiphytes (Hixon and Brostoff, 1985; Zeller, 1988).

Table 3. Grand mean density (number/m^2) of conspicuous invertebrates, by species, censused on undisturbed patch reefs (N=4 reefs in each period).

	Period			
	Initial Number/m^2 (SD)		Final Number/m^2 (SD)	
Species/taxa*:				
Echinometra mathaei	12.09	(9.43)	11.84	(8.63)
Rhynchocinetes sp.	0.42	(0)	8.95	(7.53)
Diadema paucispinum	2.98	(1.89)	4.57	(3.13)
Ophiocoma pica	0	(0)	1.89	(1.75)
Plakobranchus ocellatus	1.24	(1.18)	0	(0)
Echinostrephus aciculatus	0.89	(0.77)	0.50	(0.44)
Ophiocoma sp.	0.02	(0)	0.81	(1.20)
Heterocentrotus mammillatus	0.24	(0.30)	0.66	(0.89)
Coralliophila erosa	0	(0)	0.15	(0.16)
Harpiliopsis sp.	0	(0)	0.14	(0.05)
Shrimp sp.	0	(0)	0.12	(0.15)
Calcinus hazletti	0	(0)	0.10	(0.14)
Stenopus hispidus	0.07	(0.09)	0.09	(0.05)
Holothuria atra	0.04	(0.02)	0.08	(0)
Trapezia sp.	0.01	(0)	0.06	(0.03)
Saron sp.	0	(0)	0.05	(0.04)
Calcinus latens	0	(0)	0.04	(0.04)
Tripneustes gratilla	0.04	(0)	0	(0)
Chama sp.	0.01	(0)	0.04	(0.00)
Bivalve (abalone like)	0.04	(0)	0	(0)
Holothuria difficilus	0.04	(0)	0	(0)
Turbo sandwicensis	0.02	(0.01)	0.01	(0)
Domecia hispida	0	(0)	0.01	(0)
Actaea sp.	0	(0)	0.01	(0)
Stegopontonia commensalis	0.01	(0)	0.01	(0)
Tricolia variabilis	0	(0)	0.01	(0)
Eucidaris metularia	0.01	(0)	0.01	(0)
Linckia sp.	0.01	(0)	0	(0)
TOTAL	18.43	(13.75)	30.38	(24.31)

*Additional invertebrate species/taxa, each accounting for <0.1% of all censused on the four patch reefs: *Aplysia parvula, Conus leopardis, Pseudoboletia indiana, Galathea* sp., *Linckia guildingi, Conus* sp., *Pagurid* sp., *Antheopsis papillosa, Actinopyga obesa, Conus abbreviatus, Calcinus* sp., *Polyplectana kefersteinii, Euplica turturina, Dolabrifera* sp., *Conus lividus*, and *Lanice conchilega*.

Table 4. Mean percent of bottom covered by each major live coral species on undisturbed patch reefs (N=4 reefs in each period).

	Period			
	Initial Mean	(% SD)	Final Mean	(%SD)
Species				
Pocillopora meandrina	2.05	(2.03)	4.40	(5.30)
Porites lobata	2.32	(3.52)	0.38	(0.03)
Pocillopora damicornis	1.85	(1.99)	1.26	(0.95)
Cyphastrea ocellina	0.83	(0.54)	0.91	(0.35)
Leptastrea purpurea	0.15	(0)	0	(0)
Porites compressa	0.04	(0)	0	(0)
TOTAL	7.23	(8.08)	6.94	(6.63)

Table 5. Mean percent of bottom covered by each major algal taxon on undisturbed patch reefs (N=4 reefs in each period).

	Period			
	Initial		Final	
Species/taxa* [TYPE]:	Mean %	(SD)	Mean %	(SD)
Red algal [TURF]	21.19	(9.78)	2.79	(4.33)
Brown algal [TURF]	13.88	(2.14)	5.76	(9.12)
Spyridia filamentosa [FRONDOSE]	10.23	(11.55)	1.07	(0.77)
Dictyota sp. [FRONDOSE]	6.66	(4.78)	2.13	(2.06)
Ralfsia exponsa [ENCRUSTING BROWN]	6.32	(6.63)	6.94	(2.83)
Lobophora variegata [FRONDOSE]	3.22	(6.82)	3.62	(6.05)
Hydrolithon (*reinboldii*?) [CRUSTOSE CORALLINE]	3.26	(4.80)	1.79	(1.85)
Lyngbya majuscula [BLUE-GREEN]	2.20	(1.90)	1.01	(1.01)
Hydrolithon (*breviclavium*?) [CRUSTOSE CORALLINE]	2.06	(2.59)	1.69	(1.87)
Porolithon onkodes [BRANCHED CORALLINE]	1.16	(0.96)	0.73	(0.94)
Colpomenia sinuosa [FRONDOSE]	0.85	(0.92)	0.08	(0.04)
Turbinaria ornate [FRONDOSE]	0.84	(0.27)	1.53	(1.98)
Hormothamnion (*enteromorphoides*?) [BLUE-GREEN]	0.78	(0.13)	1.49	(1.03)
Lithophylum sp. [BRANCHED CORALLINE]	0.53	(0.38)	0.78	(1.37)
Neogoniolithon frutescens [BRANCHED CORALLINE]	0.40	(0.29)	0	(0)
Stypopodium flabelliforme [FRONDOSE]	0.31	(0)	0	(0)
Dictyosphaeria versluysi [FRONDOSE]	0.29	(0.23)	0	(0)
Hormothamnion sp. [BLUE-GREEN]	0.29	(0.29)	0	(0)
Galaxaura rugosa [FRONDOSE]	0.27	(0.26)	0	(0)
Codium arabicum [FRONDOSE]	0.25	(0.30)	0	(0)
Sporolithon (*erythraeum*?) [CRUSTOSE CORALLINE]	0.22	(0)	0	(0)
Halimeda opuntia [FRONDOSE]	0.20	(0.16)	0.11	(0)
Porolithon gardineri [BRANCHED CORALLINE]	0.17	(0.13)	0.33	(0.43)
TOTAL	76.69	(55.50)	32.21	(35.67)

*Additional algal species/taxa each accounting for <0.2% cover in either period: *Cladophora laetevivars, Laurencia nidifica, Gracilaria coronopifolia, Halymenia formosa, Dictyota acutiloba, Padina* sp., *Sphacelaria rigidula, Peyssonnelia rubra, Codium edule, Chnoospora implexa, Grateloupia filicina,* and *Padina australis.*

Other Ecological Characteristics

Large Transient Animals. Shark and jack densities are reported to be relatively high in the NWHI (all major habitats pooled), except at Midway and Kure, where apex predators were significantly lower (DeMartini and Friedlander, 2004). From an independent estimate of daily sightings, we found visits by large transient fish to the natural patch reefs to be infrequent (i.e., only one shark seen every 5.6 days of underwater surveying, and only one large jack every 4.1 days; May 1981-August 1985; N=118 field dates). Rates for summer periods (May-August) were higher (i.e., one shark every 3.8 days, and one jack every 2.9 days). Whether the presence of divers had any influence on these rates or not is unknown. Estimated sizes (mean and range) are given for species of large vertebrates in Table 6. The gray reef shark (*Carcharhinus amblyrhynchos*) predominated. Tiger shark (*Galeocerdo cuvier*) were seen occasionally around the reefs during May-July, in synchrony with peak fledging by juvenile Laysan albatross (*Diomedea immutabilis*), a prey item. Dominant jacks were *Carangoides orthogrammus*, *Caranx melampygus*, *C. ignobilis,* and *Seriola dumerili*. Less frequent sightings of other large marine vertebrates in the general Welles Harbor study area were: 26 Hawaiian monk seals, 24 rays, and 10 sea turtles (May 1981-August 1985; N=221 observation dates). About 18 spinner dolphin pods (typically 35-40 individuals) were recorded (June 1984-August 1985; N=82 dates).

Behavioral Observations. Incidental observations throughout the study helped confirm ecological associations of resident fishes. Adult spotted cardinalfish (*Apogon maculiferus*), a nocturnal zooplanktivore, typically sheltered in holes and crevices of the reef by day. Large groups of juveniles, which settled in high densities in some summers, were also common under ledges and in small caves. Newly settled Hawaiian Dascyllus (*Dascyllus albisella*) and saddle wrasse (*Thalassoma duperrey*) sheltered in branches of live *Pocillopora meandrina* coral heads as a preferred habitat. The Pacific gregory (*Stegastes fasciolatus*) defended evenly spaced algal territories several square meters in area with variable success. Small juveniles of several common species (e.g., *A. maculiferus, P. spilosoma, T. duperrey, C. ovalis*) were found sheltering in the long spines of the sea urchin *Diadema paucispinum* during peak summer settlement periods.

Fish-Physical Correlations

Midway patch reef fish assemblages were found to be dependent upon major physical characteristics of the reef substrate. Numerical abundance and species richness for all fish (combined), and abundance for each of the six most common species, showed a strong, significant correlation with reef area (strongest correlation), volume, and vertical relief (Table 7). All correlations among the three physical reef characteristics, area, volume, and vertical relief (independent of fish), were also highly significant (Schroeder, 1989a).

Table 6. Size class estimates for large (~SL ≥50 cm, in 5-cm bins) marine vertebrates sighted in Midway lagoon from May 1980 to August 1985.

Species/taxa:	Mean cm (SD)	Min. cm	Max. cm	N (individuals)
Shark:				
Carcharhinus amblyrhynchos	125 (25)	30	250	336
Galeocerdo cuvieri	255 (50)	175	370	30
Triaenodon obesus	150 (15)	120	185	4
Carcharhinus melanopterus	135	135	135	1
Jack:				
Carangoides orthogrammus	45 (10)	15	150	67
Caranx melamplygus	50 (10)	15	110	59
Caranx ignobilis	70 (25)	5	180	30
Seriola dumerili	70 (20)	15	110	27
Carangid (spp.)	60 (10)	25	100	23
Caranx cheilio	40 (10)	15	100	17
Gnathanodon speciosus	50 (5)	45	50	3
Caranx lugubris	65	65	65	1
Caranx sexfasciatus	110	110	110	1
Ray:				
Aetobatus narinari	100 (10)	50	150	13
Mobulid (sp.)	55 (5)	50	60	2
Manta birostris	100	100	100	1
Turtle:				
Chelonia mydas	60 (10)	30	150	193
Seal:				
Monochus schauinslandi	170 (20)	100	210	18
Dolphin:				
Stenella longirostris	175 (25)	100	300	18 (pods)

Table 7. Spearman rank correlation coefficients r_s relating the numerical abundance and diversity of common species visually censused with substrate physical characteristics[1] of the respective patch reefs. (N = 142 to 193 total census replicates on 10 reefs; * P < 0.05, ** P < 0.01, *** P < 0.001, ns- not significant; for the seven species the significance level designation represents the experimentwise error rate for the group of r_s: * P < 0.0073, ** P < 0.0014, *** P < 0.0001, ns- not significant.)

	Reef Substrate Characteristic		
Fish Parameter:	Area	Volume	Vertical Relief
DIVERSITY			
Species Richness	0.577 ***	0.566 ***	0.538 ***
Species Diversity (N = 32 to 36)	0.300 ns	0.120 ns	0.369 *
ABUNDANCE			
All species[2]	0.758 ***	0.731 ***	0.677 ***
Most abundant species:			
Pervagor spilosoma	0.449 ***	0.419 ***	0.365 ***
Apogon maculiferus	0.490 ***	0.542 ***	0.397 ***
Dascyllus albisella	0.483 ***	0.390 ***	0.342 ***
Thalassoma duperrey	0.664 ***	0.646 ***	0.684 ***
Stegastes fasciolatus	0.596 ***	0.548 ***	0.627 ***
Chromis ovalis	0.304 ***	0.240 *	0.245 *
Gnatholepis anjerensis	0.256 **	0.201 ns	0.091 ns

1) Pairwise r_s correlation coefficients between substrate physical characteristics considered independent of fish abundance are: 0.976*** for Area-Volume (N = 16); 0.814*** for Area-Relief (N = 18); and 0.814*** for Volume-Relief (N = 16).
2) All taxa pooled, excluding *Gnatholepis anjerensis*.

Reef Size. The size of a reef appears to be the most useful physical attribute for predicting the structure of the fish assemblage (Sale and Douglas, 1984; Ault and Johnson, 1998); in general, fish abundance and species richness increase with patch size, due to a combination of recruitment and community dynamic processes (Helfman, 1978; Luckhurst and Luckhurst, 1978; Bohnsack, 1979; Brock et al., 1979; Gladfelter et al., 1980, Anderson et al., 1981; Carpenter et al., 1981; Sale and Douglas, 1984; Clarke, 1988). In contrast, species diversity (H') did not correlate with reef size (area or volume), possibly since H' incorporates both abundance and species richness, suggesting similarity in the structure of patch reef fish communities among different size reefs. Total fish abundance decreased on Midway patch reefs experiencing major reductions in size from storm-induced shifting sand. Two common demersal species (*T. duperrey* and *S. fasciolatus*), which had the strongest correlations between fish abundance and the three substrate variables, also were characterized by low temporal variability in numbers and had a low but steady recruitment rate over a protracted season (Schroeder, 1985, 1989a). Quantitative resource requirements (e.g., food or shelter) may contribute to higher abundances of these two demersal feeders on larger reefs. The nocturnal cardinalfish, *A.*

maculiferus, had the strongest correlation with reef volume, suggestive of its dependence on dark shelter. Three species (*P. spilosoma*, *D. albisella* and *C. ovalis*) whose abundances correlated less strongly with the substrate factors were all characterized by heavy settlement and high temporal variability (Schroeder, 1985, 1989a). *D. albisella* and *C. ovalis*, which are primarily midwater planktivores (Hobson, 1974; Parrish *et al.*, 1984), may not depend greatly on benthic substrate for food; however, the reef is probably important for their shelter. The seasonally abundant goby, *G. anjerensis*, showed low correlations with reef substrate characteristics, as it occurred primarily on the rubble-sand base around the reef.

Reef Complexity. Larger reefs generally offer greater habitat complexity that can enhance juvenile and adult survival. Complexity, based on vertical relief, of the Midway patch reefs correlated strongly with fish abundance and species richness, but only weakly with species diversity. Friedlander and Parrish (1998) also showed a high positive association between substrate relief and fish abundance off Kauai. In contrast, no significant correlation between fish assemblages (based on abundance or species richness) and patch reef topographic complexity was found by Sale and Douglas (1984) or by Ault and Johnson (1998) on the Great Barrier Reef, or by Roberts and Ormond (1987) in the Red Sea. The variability of substrate complexity (i.e., frequency of peaks in the vertical relief index [=sd]) also determines reef surface area and can affect fish parameters as well (Dahl, 1973; Luckhurst and Luckhurst, 1978).

Reef Isolation. In our study, patch reef size and isolation varied independently, while a strong size effect may have obscured any fish patterns due to isolation. Bohnsack (1979) found that numbers and species of fish on small patch reefs increased significantly with isolation, but the effect was less pronounced on large reefs. Higher juvenile fish densities found on more isolated reef patches (Schroeder, 1987, 1989b) may be due to preferential settlement (Walsh, 1985), lower predation risk (Shulman, 1985), and less interference by neighboring reef fish (Bohnsack, 1979). Settlement and post-settlement processes appear less important for more vagile fish species (e.g., lizardifish) that move among isolated reef patches, apparently guided by habitat preferences or resource availability (Ault and Johnson, 1998).

CONCLUSION

Coral reef communities are complex and dynamic, even at the scale of small patch reefs. In our study at Midway, major differences and changes in reef physical attributes significantly influenced fish assemblages. While most taxa of nonteleost reef biota (e.g., visible macroinvertebrates, corals, algae) exhibited considerable spatial and temporal variability, it was not obvious that any of these differences produced major variation in the fish communities. But finer-scale processes (e.g., a species' juvenile life stage affected in a particular season) may be operating and significant. It is important to supplement studies of coral reef ecosystems with detailed information on pertinent physical, biological and ecological variables, since these factors may have the potential to mask more subtle ecological processes. Our ability to model and predict potential impacts of harvesting or other human activities, and related ecological ramifications thereof, will require a much better understanding of the structure and functional processes of these unique and valuable systems. Information presented here on ecological characteristics of coral patch reef communities should be useful as a reference for more contemporary ecosystem studies in the NWHI, as well as comparison to other patch reefs within the NWHI and in other geographic regions.

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